The Larval Gills of the Odonata.

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The rectal gills of *Libellula* and *Æschna* are well known to every student of comparative anatomy, and have attracted much attention since they were first discovered by Swammerdam. Chun's paper on the so-called "rectal glands" of Insects * is usually quoted as the most complete account of their structure. The works of our predecessors, however, have left room for new researches, and certain important physiological considerations remain unnoticed.

Wherever the respiratory organs of terrestrial Arthropods consist of numerous lamellæ enclosed in a recess or cavity, there is some structure present to prevent their adhering to one another, some provision for keeping open the spaces between these lamellæ, and allowing the air, or water, to freely bathe their surfaces. In the so-called lungs of spiders and scorpions, for instance, the lamellæ bear on one face at least numerous chitinous rods or ramified arborescent prominences †. We were, therefore, surprised not to find in the works of our predecessors any mention of the existence of such an apparently necessary mechanism in the Odonata. We soon discovered, however, that the gills of these insects are no exception to the rule. In *Libellula depressa* each lamella bears three conical pillars, two on one face and one on the other (fig. 1). The use of these pillars is obviously the same as that of the prominences of the Arachnidan lung; but, while the latter are only cuticular and merely more or less complex thickenings of that layer, the pillars of Odonata are outgrowths of the cuticle, followed by the subcuticular layer and containing several nuclei.

The gill of *Libellula* and *Æschna* is a leaf-like folding of the proctodæal epithelium and cuticle. The space between the two laminæ contains the main tracheal trunks. These divide very

* Chun, "Ueber den Bau die Entwickelung und physiologischen Bedeutung der Rectaldrüsen bei den Insekten." Abhandl. der Senckenb. naturf. Gesel., 10 Bd., 1876.

† See L. Berteaux, "Le Poumon des Arachnides." 'La Cellule,' tom. v. fasc. 2.

soon into a bundle of very fine tubes that neither divide again nor end freely, as is the case in other organs, but bend into a series of very long, curved, intra-lamellar loops. These loops, running parallel to the surface of the gill, reunite to form other main trunks which shortly leave the lamella and open into some branch of *the same* main tracheal tube that gives off the original trunks from which they are derived (fig. 2). As this is so, the

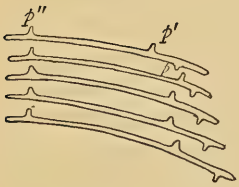

Fig. 1.

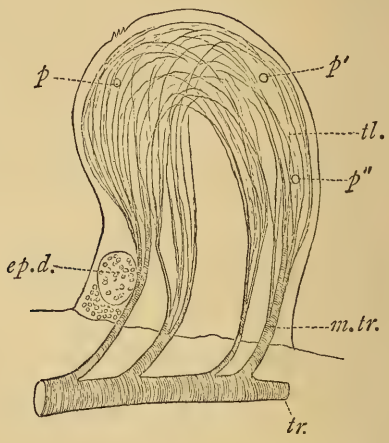

Fig. 2.

Libellula depressa.

Fig. 1.—Schematic sections through five larval gills. *p*, *p'*, *p''*, pillars.

Fig. 2.—Surface view of one gill. *p*, *p'*, *p''*, pillars. *tl.*, tracheal loops. *m.tr.*, main tracheal tubes. *tr.*, external tracheal trunk. *ep.d.*, epithelial disc.

air would not appear to circulate regularly through the system of tracheal loops, as might be supposed to be the case if the main lamellar trunks were branches of larger tubes coming from different parts of the body. The contents of the loops must be renewed, if at all, by some special mechanism, but we do not here propose to further investigate this point.

The tracheal loops, which evidently constitute the functional part of the system, do not hang freely in the space between the two laminæ: they enter the subcuticular layer and run their whole length through it, usually not in contact with the outer cuticle (fig. 3).

The subcuticular layer is a syncytium in which no cell-boundaries can be detected. It contains two kinds of nuclei, and

seems to be the result of the association and complete fusion of two distinct elements—the subcuticular epithelium and the tracheal cells.

As before remarked, the gills contain an intralamellar cavity in which the tracheal tubes are lying. The existence of this cavity was not easily observable, as the two plates of the

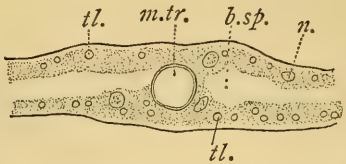

Fig. 3.—Part of section through a rectal gill.

tl., tracheal loops within the subcuticular layer. *m.tr.*, main tracheal tube. *b.sp.*, blood-space. *n.*, nucleus.

lamella, in sections of hardened objects, are usually found sticking tightly to each other. We endeavoured to determine its limitations by cautiously injecting Indian ink into the "body-cavity." The black particles were found between the two plates up to the free edge. The existence of the cavity may, however, be sometimes detected without any injection, and, even when the plates are in contact, blood-cells are sometimes noticeable between them. There is, therefore, not the slightest question about the existence of an intralamellar cavity communicating with the cœlom, and the presence of blood in the gill cannot be doubted. The necessity for definitely establishing these points is sufficient when it is remembered that the process of respiration would appear to be very different in a "bloodless" gill from what it is in an organ supplied with an elaborate blood-system.

The tracheal loops of the gill were known to Leydig, and were first described by Oustalet *. But no one, so far as we know, has ever noticed that they are enclosed within the protoplasmic layer. Such gaseous interchange as takes place between the contents of the tracheal loops and the exterior must first involve this protoplasmic layer; and this fact appears to us important in its bearings on the conclusion now gaining ground, that

* Oustalet, "Mémoire sur la respiration des larves des Libellules." Ann. Sci. Nat. sér. 5, Zoologie, tom. 11 (1869).

the absorption of oxygen is not a mere physical process but a more complex one, in which the living protoplasm plays an active part. It has been experimentally shown that the death of the epithelial cells causes a striking change in the action of an organ functioning, during life, as an osmotic divider between two different liquids or gases. As Professor Miall very rightly remarks, the first setting up of the process in young larvæ, when small bubbles of gas appear in the liquid that fills the tracheal tubes, cannot possibly be explained as a mere physical phenomenon. Whatever may be the mechanism of respiration, it is a process much more intricate than the play of an ordinary osmotic apparatus; a process that deserves the term "vital," which we are wont to apply to complex activities, the actual workings of which escape our observation. The living protoplasm is the agent of absorption and setting free of the oxygen as well as of the emission of carbonic acid.

No wonder, therefore, that in the gills of Odonata the functional air-tubes are completely imbedded in the protoplasm of the subcuticular layer. And, as regards the absorption of oxygen, there is no wonder that no special mechanism is provided to renew or to remove the contents of the tracheal loops. If the oxygen extracted from the surrounding water is actively discharged into the tracheal cavity by the protoplasm, and a stream of gas is continually blown out of the loops into the general tracheal system, no external mechanism is wanted to clear out the gaseous contents of the gill and transmit the oxygen to the other parts of the body.

As regards the emission of carbonic acid a difficulty arises; for if the function of the gill be to excrete the carbonic acid as well as to absorb the oxygen, it seems likely that the former must be carried to the organ by some mechanism. If the tracheal tubes furnished the only apparatus through which the carbonic acid could be carried, it seems that a "propelling" mechanism, though unnecessary as regards oxygen, would be required. But this is not the case. Carbonic acid is carried away from the organs *by the blood* and the blood-system enters the gills, as we have said before. There it may be directly absorbed and ejected by the subcuticular layer without ever entering the functional part of the tracheal system. The only objection to this view is that the blood is not very abundant in the gill, and that no special mechanism is known to make it circulate through the organ.

We hope to show in a subsequent paper, however, that the existence of such a mechanism is quite possible though it cannot be very efficient. Being thus led to enquire whether there are no other organs to help in the excretory activity of the gill, we have discovered, and intend soon to describe more fully, two very remarkable and quite enigmatical organs in a part of the digestive tract, which we propose to term the *prærectal vesicle.*

The organs in question consist of two discs of very peculiar epithelial cells which depend from the wall of this vesicle. They appear to be non-glandular, and their function is quite unknown. We have on several occasions found the prærectal vesicle filled up and considerably swollen by a gaseous contents, and we incline to the belief that the function of the "discs," as well as of other productions in the basal part of the gill which are covered with the same epithelium, may be the excretion of carbonic acid, but we put this forward merely as a hypothesis, pending experimental research on the subject.

In all non-tracheal gills, as well as in Arachnidan lungs, the blood plays a very important part indeed in the process of respiration—that of collecting and carrying away the oxygen to all parts of the body. The osmotic process, on current theory, is supposed to take place between the outer atmosphere or water and the blood itself, through the cellular and cuticular wall. Now, if there is a blood-space in the gill of *Libellula*, it may be thought likely that the same process must take place there, just as in the gills of *Limulus* and *Isopods*, or in the lungs of spiders, because the same causes must produce similar effects under similar circumstances, and a certain foundation cannot be refused this hypothesis. We may remark, however, that the circumstances are not exactly the same in tracheal and non-tracheal organs. The presence of numerous tracheal loops in the protoplasmic coating of the gill may alter considerably the conditions of the process, and it could alter them even if it were a mere physical one. But, knowing that this respiratory process is neither so clear nor so simple as it is often said to be, we cannot refrain from thinking that the functional protoplasm casts the greatest part of the absorbed oxygen, if not the whole of it, into the tracheal tubes that must carry it to every organ in the body, and that the blood would seem to play a very unimportant part, if any, in the absorption of that gas. On the other hand, it must

play a very important part in the excretion of carbonic acid, for it has been shown before, and it should not be forgotten, that its function in the gill is largely that of nourishing the tissues.

To recapitulate:—

1. The rectal tracheal gills of larval Odonata are prevented from adhering to one another by the presence of three conical pillars.
2. The main tracheal tubes alone are lodged between the two plates that form the gill; the terminal loops, *i. e.* the functional parts of the system, run *within* the protoplasm of the subcuticular layer.
3. A blood-space communicating with the "body-cavity" exists in the rectal gills.
4. The oxygen seems to be absorbed through the tracheal loops by the action of the subcuticular protoplasm only, and to be discharged from these into the general tracheal system.
5. Carbonic acid, on the contrary, appears not to be carried to the gills by the tracheal tubes but by the blood alone, certain enigmatical organs borne upon a "prærectal vesicle" being perhaps directly concerned in its excretion.
6. In any case the blood would appear to play an important part in the excretion of carbonic acid, and a very unimportant one in the absorption of oxygen.